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Natural reproduction of red pine (*Pinus resinosa* ait.) in Newfoundland

B.A. Roberts

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Newfoundland and Labrador Region

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NATURAL REPRODUCTION OF RED PINE (*PINUS RESINOSA* AIT.) IN NEWFOUNDLAND

by B.A. Roberts

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ABSTRACT

This report presents results of an Island-wide investigation of the reproduction and regeneration of Newfoundland natural red pine (Pinus resinosa Ait.) stands. Red pine is the rarest coniferous tree species in Newfoundland and is known from only 22 stands. Newfoundland red pine trees produce adequate seed crops with a time lag of 21-28 days in all phases from bud break to pollination to maturity of cones and seeds when compared to Ontario due to late spring conditions. This study showed only minor differences in cone development between stands with the better site quality stands usually producing the best quantity and quality of seed. The lack of red pine regeneration in Newfoundland can be attributed to poor seedbed conditions. Aspects of the physical and allelopathic effect of the understory of Kalmia vegetation are also discussed in this report.

RÉSUMÉ

Le présent rapport décrit les résultats d'une enquête sur la reproduction et la régénération des peuplements naturels de pin rouge (Pinus resinosa Ait.) menée sur toute l'étendue de Terre-Neuve. Le pin rouge est le conifère le plus rare de l'île avec seulement 22 peuplements. Même si l'arrivée tardive du printemps entraîne un retard de 21 à 28 jours sur l'Ontario à toutes les étapes de la reproduction (éclosion des bourgeons, pollinisation et maturité des cones et des graines), les pins rouges terre-neuviens produisent un nombre adéquat de rejetons. L'étude ne fait état que de différences mineures au niveau du développement des cônes entre les divers peuplements, les mieux exposés produisant ordinairement les graines les meilleures et les plus abondantes. La faiblesse régénérative des pins rouges de Terre-Neuve peut être attribuée à un lit de semence peu favorable. Divers aspects de l'effet physique et allélopathique du sous-étage de plantes du genre Kalmia sont aussi abordés dans ce rapport.

TABLE OF CONTENTS

	Page
ABSTRACT	i
RÉSUMÉ	i
LIST OF TABLES	iii
LIST OF FIGURES	iv
INTRODUCTION	1
DISTRIBUTION AND SITE CHARACTERISTICS OF NEWFOUNDLAND RED PINE	2
RED PINE - MAJOR AND MINOR VEGETATION AND ECOLOGICAL POSITION OF THE RED PINE FOREST TYPE	8
Vegetation	8
MATERIALS AND METHODS	14
Cone Growth and Seed Production	14
Regeneration Survey	16
REVIEW OF LITERATURE	16
RESULTS AND DISCUSSION	18
Cone Growth	18
Seed Production	25
Regeneration Survey	31
CONCLUSIONS	33
REFERENCES	34

LIST OF TABLES

		Page
1.	Natural red pine stand locations, map and air photo references, aerial extent and estimates of the number of trees in each stand	4
2.	The three major red pine site types based on landform and soil characteristics for the red pine cover type of Newfoundland	5
3.	Cone development dates 1978-81 for the western (H & BN) and eastern (PA & TN1) red pine stands	19
4.	Mean monthly temperatures (°C). April-September from 1978-81. Column A - Deer Lake Station; Column B - Terra Nova Park Station	24
5.	Cone and seed statistics for 15 natural red pine locations in Newfoundland	26
6.	Cone and seed statistics from 15 red pine locations ranked by placing the means in numerical order by the Student-Newman-Keul's test. The lines indicate means that are not significantly different at the five percent level	27

LIST OF FIGURES

		Page
1.	The location of all known red pine stands (modified from Roberts, 1985)	3
2.	The location of the 11 red pine sites area I. Code names are those shown in Table 1	6
3.	Detailed map showing the four stands of red pine in central Newfoundland, geographical line II. Code names are those shown in Table 1	7
4.	The location of the seven red pine sites in northeast central Newfoundland. The stand code names are those shown in Table 1.	9
5.	Ecological position of red pine forest types in Newfoundland (modified from Damman 1964)	10
6.	Dense ericaceous shrubs in red pine understory. Kalmia and other ericaceous shrubs occupying 100% of the red pine ground cover or understory; some red pine regeneration have established and are slowly growing up through the dense ground cover; (a) SL5; (b, c) F(c) and SL6	12
7.	(a) Typical very rapidly drained Cladonia Kalmia red pine stand on coarse sandy soils. The ground vegetation is dominated by Kalmia angustifolia and Cladonia lichens as well as some stunted black spruce and sparse regeneration (SL7)	13
	(b) Red pine stand showing the very dense cover of ericaceous shrubs, however regeneration, although sparse, was present	13
8.	Developmental stages of male pollen cones of red pine in Newfoundland	20
	(a) Male pollen (staminate) cone developing in groups around the base of vigorous twigs, June 8, PA site.	
	(b) Male pollen cones (x 3), purple compact, 21-22 June, PA site.	
9.	Developmental stages of male pollen cones of red pine in Newfoundland	21
	(a) Swollen scarlet red staminate cone, 25-27 June, PA site.	
	(b) Mottled red-yellow pollen cones as they become ripe and start to shed pollen grains, 27 June, PA site.	
	(c) After pollen grains shed the pollen cones or staminate strobili are golden brown. One week after shedding, PA site.	

LIST OF FIGURES (Concl'd.)

Page

10. Developmental stages of female seed cones of red pine in Newfoundland 22
    (a) Female seed cones develop at the ends of twigs 14-18 days after the staminate flowers first appear, PA site.
    (b) Closed blue female conelet which has entrapped the male pollen, 26 July, PA site.
    (c) Overwintering conelets which have turned brown, PA site.
    (d) Semi-mature green cone almost fully grown 4-5 cm long. First week of August, PA site.

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NATURAL REPRODUCTION OF RED PINE (*PINUS RESINOSA* AIT.) IN NEWFOUNDLAND

by

B.A. Roberts

INTRODUCTION

Red pine, *Pinus resinosa* Ait., the rarest indigenous coniferous tree species in Newfoundland is known from only twenty-two stands located in three distinct geographic parts of the Island (Roberts 1981, 1985). Stands vary from small ones with only a few red pines to those exceeding 100 ha with several thousand trees. In Newfoundland it usually grows on sands and gravels of glacial outwash or on lake bottom deposits. It has good potential for planting on these course textured glacial outwash or lake bottom sites where it will produce much more volume (two to three times) than black spruce at the same rotation. It also has good potential on upland dry knolls and river terraces, and can grow under moderate exposure and low nutrient conditions.

The main objectives of this study were to investigate, in Newfoundland red pine, the various sexual reproductive phases leading to seed production; to determine if there were differences in cone development amongt the various stands, and to establish that Newfoundland red pine produces viable seeds. The lack of regeneration in the Newfoundland sites might then be related to other factors, such as seedbed condition. The timing of seed crops is very important when considering regeneration after fire or cutting, and is essential in understanding stand dynamics.

DISTRIBUTION AND SITE CHARACTERISTICS OF NEWFOUNDLAND RED PINE

Red pine has a wide distribution primarily in Northeastern North America and ranges from Newfoundland in the east to West Virginia, west to Manitoba (Fowells 1965; Roberts 1985). One of the earliest red pine distribution maps was published in 1911 (Fernald 1911) and that report postulated that the drought tolerant red pine successfully migrated from coastal New England to Newfoundland via islands of land along the eastern seaboard. The distribution map for Newfoundland published by Damman (1976) reported eight known locations in two different parts of the Island.

Red pine is still the rarest coniferous tree species in Newfoundland occurring at only 22 natural locations (Figure 1, Table 1). As a result of a recent study (Roberts 1985) 14 new locations of red pine have been mapped. The broad pattern of distribution in three geographic lines of occurrence suggests that the species was once more common on the Island and had a range approximately the same as white pine. The stands today contain about 15 000 mature and semi-mature red pine trees which occupy portions of 1000 ha (Table 1). Regeneration of red pine is sparse in most stands. Only two large stands exist of 3-5000 trees; four medium stands 500-1500 trees and 10 small stands 100-500 and six very small stands have less than 50 red pine trees.

Red pine usually grows on sands and gravels of glacial outwash or on lake bottom deposits. The mineral soils under these stands are nutrient-poor coarse-textured Ortstein Humo-Ferric Podzols, and Orthic Humo-Ferric Podzols (Roberts and Bajzak 1984) (Table 2). Stands near Birchy Lake (OS) (Figure 2) and at Charles Arm (CA)(Figure 3) are on

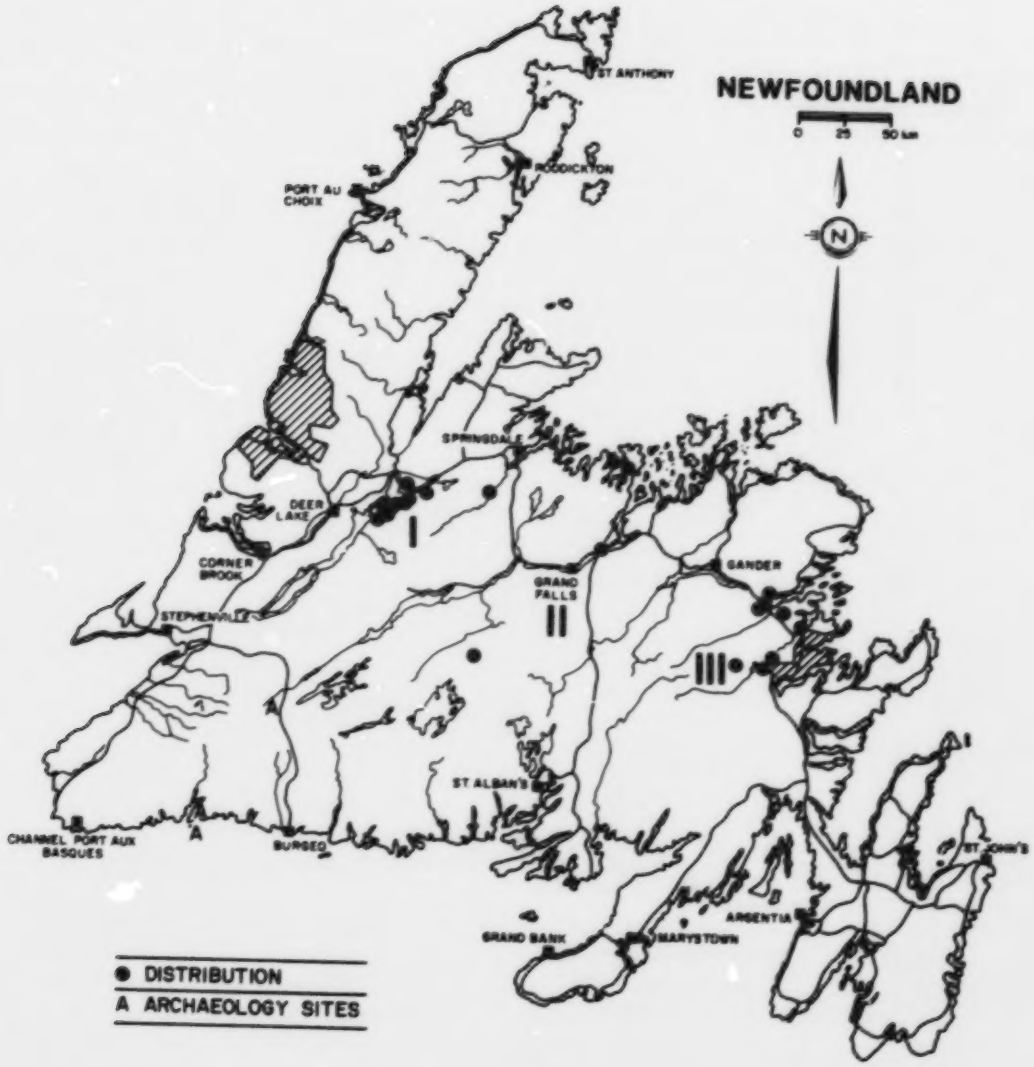


Figure 1. The location of all known red pine stands (modified from Roberts 1985).

Table 1. Natural red pine stand locations, map and air photo references, aerial extent and estimates of the number of trees in each stand.

Stand name	Map reference	1:50,000 Map sheet	Air photo 1:12,500	Approx. area* (ha)	Approx. No. of trees
1. Howley (H)	932-468	12 H/3 Deer Lake	NF 78040-68	< 15	< 650
2. Sandy Lake (SL1)	950-475	12 H/3 Deer Lake	NF 78040-69	< 20	< 1000
3. Sandy Lake (SL2)	963-486	12 H/3 Deer Lake	NF 78040-128	< 5	< 250
4. Sandy Lake (SL3)	988-498	12 H/3 Deer Lake	NF 78040-125	< 5	< 350
5. Sandy Lake (SL4)	023-528	12 H/2 The Topsails	NF 78041-26	< 5	< 200
6. Sandy Lake (SL5)	033-535	12 H/2 The Topsails	NF 78041-150	< 5	< 200
7. Sandy Lake (SL6)	047-541	12 H/2 The Topsails	NF 78041-203	< 5	< 200
8. Sandy Lake (SL7)	055-548	12 H/2 The Topsails	NF 78041-202	< 10	< 250
9. Birchy Narrows (BN)	098-588	12 H/7 Sheffield Lake	NFA 31077-9	< 1	< 25
10. Old Stand (OS)	207-632	12 H/7 Sheffield Lake	NF 78058-58	< 1	< 15
11. Rowsells Brook (RB)	489-582	12 H/8 Springdale	NFA 31076-164	<200	< 3000
12. Overflow Brook (OB)	541-810	12 A/9 Noel Paul's Bk.	NFA 31131-200	<100	< 1500
13. Exploits River (ER)	147-319	2 E/3 Botwood	NFA 31034-5	< 1	< 15
14. Charles Arm (CA)	246-687	2 E/6 Point Leamington	NFA 31106-73	< 5	< 300
15. Strong Island Sound (SIS)	227-731	2 E/6 Point Leamington	NFA 31106-35	< 5	< 100
16. David Smallwood Pk (DSP)	042-090	2 D/16 Gambo	NF 78018-1	< 5	< 150
17. Mint Brook (MB)	007-017	2 D/9 Glovertown	NFA 31109-142	< 1	< 15
18. Pine Acres (Grants Pit) (PA)	080-015	2 D/9 Glovertown	NFA 311069-154	<400**	< 5000
19. Traytown (TT)	948-798	2 C/12 Eastport	NFA 31108-79	< 5	< 50
20. Georges Pd. (GP)	889-753	2 D/9 Glovertown	NF 78030-125	< 20	< 500
21. Terra Nova 1 (TN1)	060-756	2 D/9 Glovertown	NFA 31096-177	< 2	< 50
22. Terra Nova 2 (TN2)	034-750	2 D/8 Port Blandford	NFA 31096-180	< 50	< 250
TOTALS				<866	<14070

* Area of the land form.

** < 100 ha is reserved by the Provincial Government with the remaining 300 ha privately owned.

Table 2. The three major red pine site types based on landform and soil characteristics for the red pine cover type of Newfoundland.

Red pine site type	Soil parent materials and landforms	Soil* drainage	Soil subgroup*
1. Red pine on medium textured sands (RP1)	Sandy loam, glaciofluvial terraces or glaciofluvial plain	2	Orthic Humo-Ferric Podzol
2. Red pine on coarse textured glacio fluvial deposits (RP2)	Loamy sand, glaciofluvial terraces or eroded glacio-fluvial terraces	1	Ortstein Humo-Ferric Podzol/or Duric Humo-Ferric Podzol
3. Red pine on Folisols over bedrock (RP3)	Dry organic FH/rock	1	Lithic Folisol/ bedrock

*As per the Canadian Soil Classification System 1978.

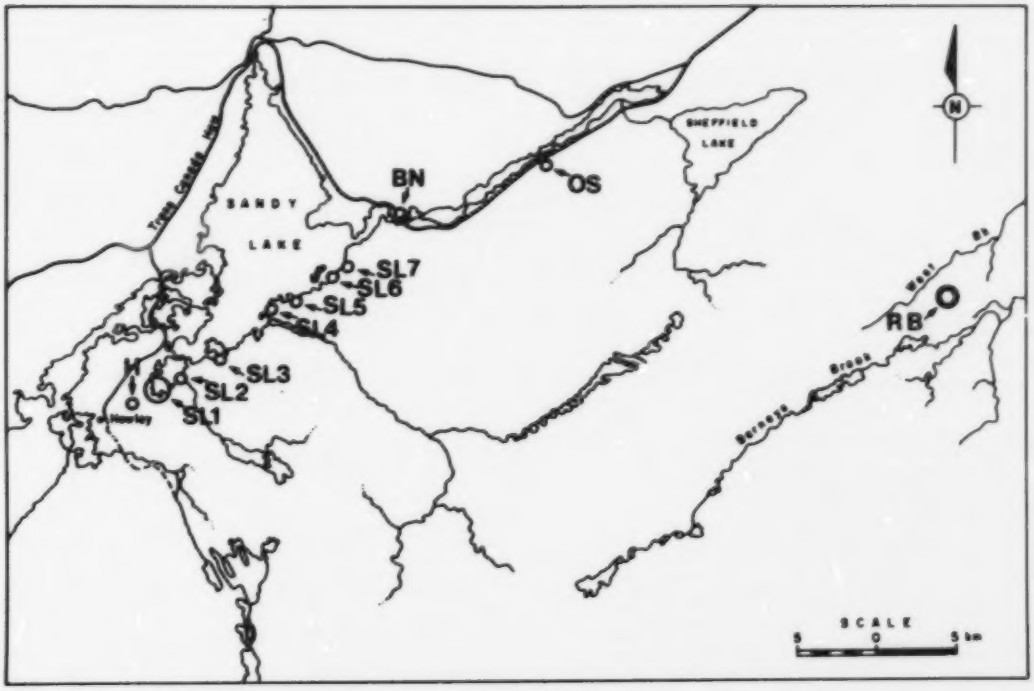


Figure 2. The location of the 11 red pine sites area I. Code names are those shown in Table 1.

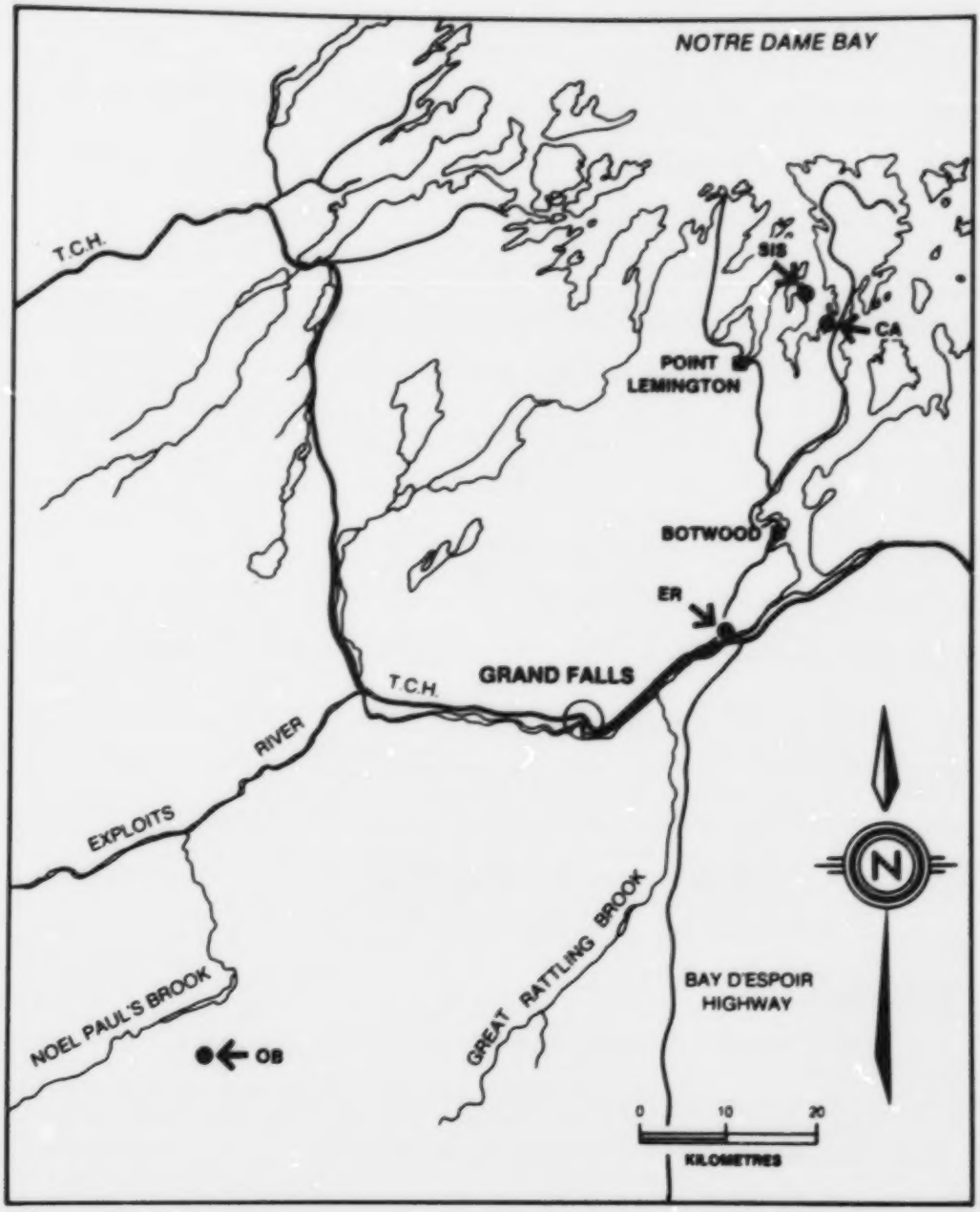


Figure 3. Detailed map showing the four stands of red pine in central Newfoundland, geographical line II. Code names are those shown in Table 1.

bedrock or shattered bedrock with some mor humus cover and the soils are Organic Folisols. There are three major site types (Table 2) in Newfoundland with RP2 the most common. Grants Pit or Pine Acres (PA), the largest and best known stand, is an ecological reserve (Figure 4).

RED PINE - MAJOR AND MINOR VEGETATION AND ECOLOGICAL POSITION OF THE RED PINE FOREST TYPE

A forest site classification has been conducted for most of Newfoundland, e.g., central (Damman 1964). The major limitations to forest growth are the availability of moisture and the natural fertility of the site. Damman (1964) graphs the relationship for the forest types of central Newfoundland. If we use this framework the ecological position with respect to the variables of moisture and fertility for the red pine forest type can be shown. Figure 5, modified from Damman (1964), shows the red pine forest type in the same position as the Cladonia-Kalmia black spruce and essentially the red pine occupies the driest and most nutrient poor sites.

Vegetation

The red pine forest type is semi-open in terms of tree density with red pine occupying 50-75% cover in the larger stands to 5-25% cover in the very small stands. Seven other tree species occur, but most of these have less than 5% cover in the stands where they occur.

Black spruce occurs in every stand, sometimes in equal number to red pine. A succession of the red pine forest type to black spruce type after fire or logging is thus a real possibility in most stands.

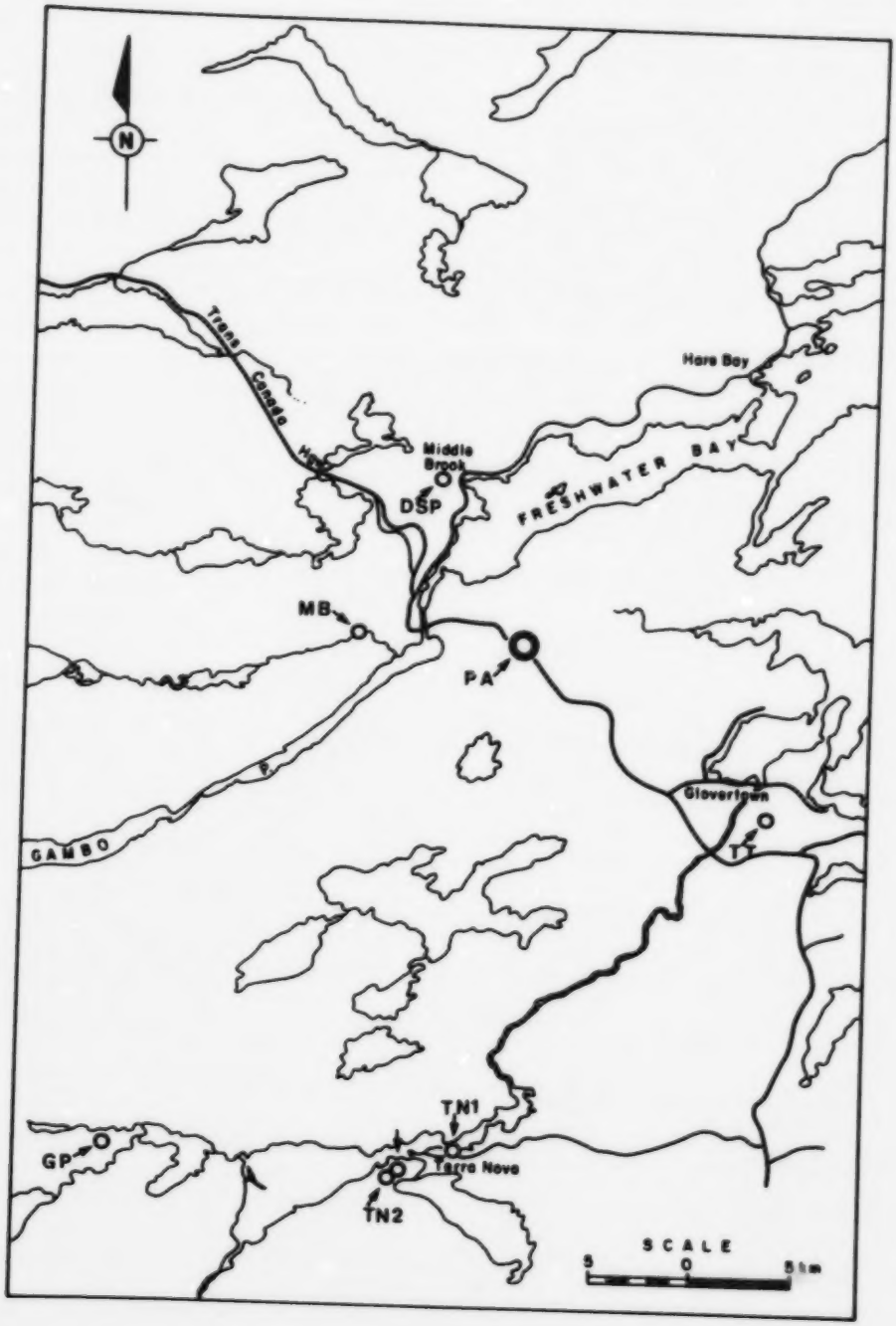


Figure 4. The location of the seven red pine sites in northeast central Newfoundland. The stand code names are those shown in Table 1.

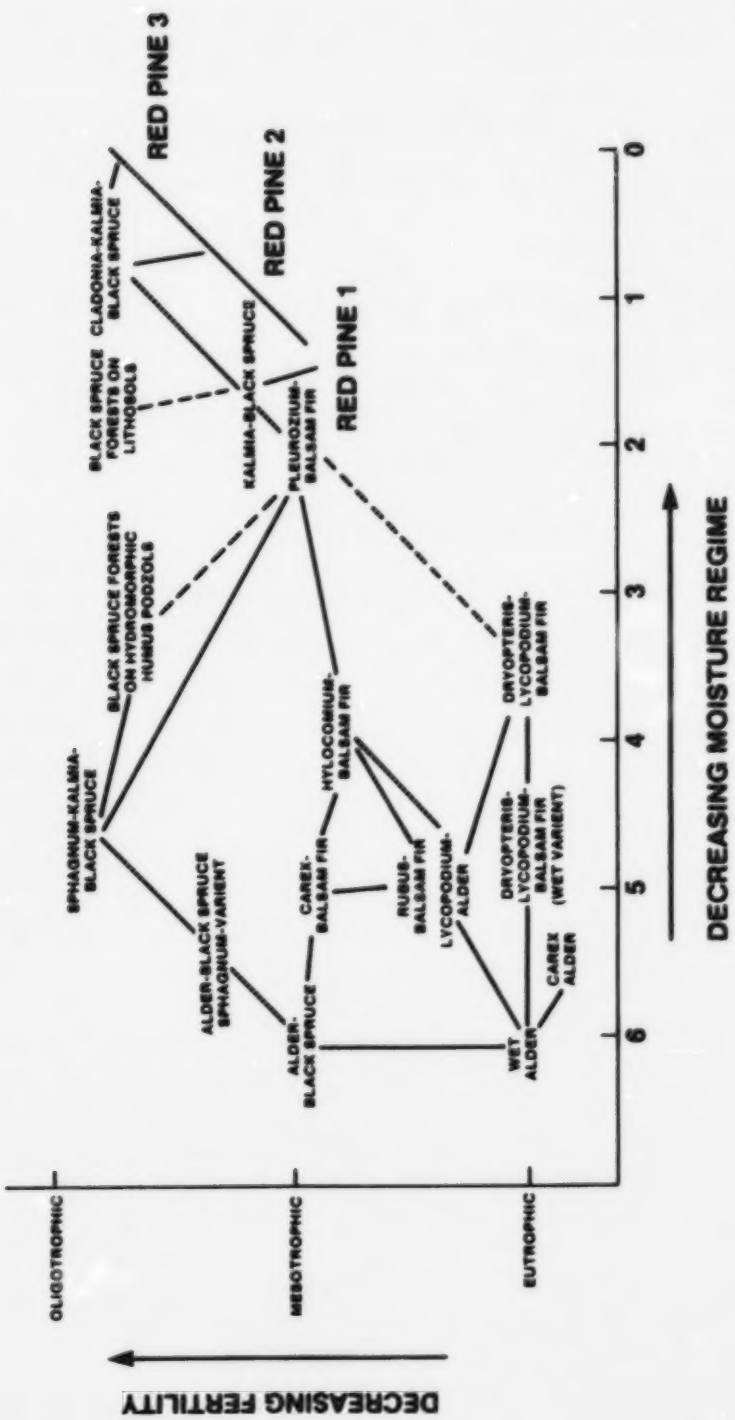


Figure 5. Ecological position of red pine forest types in Newfoundland (modified from Damman 1964).

White pine occurs in all stands except the SIS site, but is much less abundant than red pine. White pine is known to have a greater ecological amplitude than red pine (Dansereau, 1953), but red pine can thrive on sites too poor for white pine.

The dominant minor vegetation associated with the red pine forest in nearly all stands is Kalmia angustifolia, consistently occupying 50-75% of the ground cover. Other ericaceous shrubs which dominant 20-50% of the ground cover are Rhododendron canadense, Vaccinium angustifolium, V. vitis-idaea, and Ledum groenlandicum. The Cladonia lichens are very common in almost all stands (Figure 6a) and have some relevance to fire frequency.

The ericaceous shrubs, particularly Kalmia angusitfolia and Rhododendron canadense, are successful after fire and grow well in the open-grown red pine stands, often reaching heights greater than 1 metre (Figure 6b). The dense cover of the ericaceous shrubs makes regeneration of red pine difficult on such sites, but not impossible (Figure 7). The timing of fire and seed crops, and the growth of ericaceous shrubs are factors which greatly influence regeneration.

The mor humus usually associated with the ericaceous type of ground cover is often very shallow, averaging 5-7 cm in stands that have several fire-scarred red pines and 10-12 cm in stands that have not been burnt since 1900. If more moisture was available on these sites, the mor humus would be thicker due to faster rhizome growth. The litter quantity

Figure 6. Dense ericaceous shrubs in red pine understory. Kalmia and other ericaceous shrubs occupying 100% of the red pine ground cover or understory; some red pine regeneration have established and are slowly growing up through the dense ground cover; (a) SL5; (b, c) SL6 site.

Figure 7. (a) Typical very rapidly drained Cladonia Kalmia red pine stand on coarse sandy soils. The ground vegetation is dominated by Kalmia angustifolia and Cladonia lichens as well as some stunted black spruce and sparse regeneration (SL7).

(b) Red pine stand showing the very dense cover of ericaceous shrubs, however regeneration, although sparse, was present.

is slightly greater in the stands which have received recent fire, where there is more shedding than the normal third to fifth year needles, due to crown scorch.

MATERIALS AND METHODS

Cone Growth and Seed Production

Four stands of red pine of known site quality (Roberts and Bajzak 1984, Roberts 1985) (Terra Nova 1, Pine Acres, Birchy Narrows, Howley)(Table 1) were chosen for detailed observations because of their accessibility and because they represented the eastern and westernmost stands. These stands were visited every two to three days from 7 May to 30 July, then weekly till the end of October from 1978-81 inclusive. Observations such as bud swell, first green, first male cone, colour, size and pollen shedding, were recorded at the four stands on a prepared phenology data card. At each site ten dominant or codominant trees were climbed to the upper crown position for observations of cone development and measurement.

The cone development of other stands was also noted when they were visited during the course of other fieldwork. In addition to direct observations of cone development in the field, each of the phenological stages was photographed in colour. Single 25 cm branch samples were taken for measurements of the shoot, microsporangiate and megasporophyll stages to the mature cone stage. At least 100 measurements were made on the size of each conelet stage.

Because of the approximately two-year period in which it takes the red pine cones to produce seed, one is able to predict the cone crop for subsequent years. In late 1977, there were many female cones in their first post-bud year at most red pine stands in Newfoundland, and thus a good to bumper cone crop was assured for 1978. Cone collections were made to evaluate seed yields at 15 red pine locations in the second week of October, 1978. At least 250 cones were collected from each tree by climbing. Sampling of cones from dominant and codominant trees was confined to the upper portion of the crown and the outer apex of the tree because cone size in red pine decreases with increasing distance from the apex of the tree (Lyons 1956).

Fresh cones from each lot were observed in the field for evidence of insect damage, disease and resin. The number of cones per litre was measured to evaluate cone size change from stand to stand. Cones were placed in labelled paper bags and stored at 2-3°C. Twenty-five unopened cones were selected at random from each cone lot, and the lengths and widths measured. Each cone was then air-dried for four weeks at 25 ± 4°C in a separate bag. The centre of each cone was then drilled, to facilitate removal of all seeds, wings, and scales and to check for possible internal insect feeders, etc. The oven-dry weight of all the cone matter without seeds was obtained after drying at 60°C for 48 hours. The following were also measured: total number of full seeds per cone, number of unfertilized seeds (wings) per cone, weight of 1,000 seeds, and percentage of full seeds that germinated. The germination capacity was derived after 500 seed lots from each of fifteen stands were

germinated on moist filter paper in covered petri dishes at 23 ± 2°C. Germination counts were made twice a week for five weeks, and non-germinated seeds were cut to determine the proportion of full seeds not germinating. A greenhouse experiment was initiated to assess early growth differences among stands. Seeds were sown to exact depths in a replicated split block design. However, during the tenth week greenhouse temperatures rose to 44°C causing mortality of some seedlings. The percentage of seedlings emerging in the seed pots is the only data given.

Regeneration Survey

At each of the twenty stand locations several transects were laid out to assess the regeneration of young pines. The number of transects increased with the size of the stand. Along the transects regeneration was tallied in 1 m^2 quadrats established every 10 m. Regeneration was rated good if 50-80% of quadrats were stocked, medium if 20-49% were stocked, and poor if less than 20% were stocked. The size of each red pine stand map reference, code names for each and approximate numbers of mature trees in each stand are given in Table 1.

REVIEW OF LITERATURE

Red pine is exceptionally uniform morphologically (Rudolf 1957; Fowler and Heimburger 1969; Fowler and Morris 1977). Small but statistically significant differences among trees from different seed origins in respect to survival, phenology, growth rate, wood quality, photoperiodic response have been demonstrated (Fowler and Heimburger 1969). The feasibility of genetic improvement (Fowler and Lester 1970) is predicated

on incorporation of small amounts of genetic gain into large numbers of seedlings.

One of the main constraints to using red pine as a reforestation species in the past was the scarcity of seed supply from natural stands (Fowler and Heimburger 1969). Cones with viable seed can occur in trees as young as 12 years, but 20-25 years is considered the minimum cone bearing age, and 50-150 years the optimum (Horton and Bedell 1960). A good cone crop occurs every 3-7 years, bumper crops every 10-12 years, and a light crop in most intervening years (Horton and Bedell 1960). Cones of red pine can be artificially ripened seven weeks before natural seed dispersal (Winston and Haddon 1981) and seeds can remain viable for more than 30 years if stored at 1-3°C (Wang 1974). There is however little work reported on the demography of forest tree seed (Cavers 1983).

Cone production in red pine is greatly affected by stand density, and can be stimulated by heavy thinning of closed stands (Stiell 1971). Studies in northern Wisconsin (Lester 1967) showed that cone crop size was highly correlated with temperature at the time of or prior to cone initiation. Frost killing of developing red pine female strobili (seed cones), resulting in cone crop failure also has been reported (Schooley et al. 1986).

Red pine is monoecious, with male and female strobili occurring on the same tree. Cone morphogenesis has been studied cytologically (Duff and Nolan 1958). Cone primordia can be initiated about the mid point of the growing season of the preceding year (July in Ontario)

(Horton and Bedell 1960). Buds containing partially differentiated microsporangiate (pollen) cones are recognizable in autumn by their greater diameter in relation to length and whole buds containing ovulate cone primordia can sometimes be identified by touch in autumn (Fowler and Lester 1970).

RESULTS AND DISCUSSION

Cone Growth

Male pollen cones developed in groups around the base of vigorous twigs and were first visible as early as 6 June (Table 3, Figure 8). The pollen cones or microsporangiate strobili progressed from a compact deep purple (Figure 8) in mid June to a swollen scarlet red by the third week of June, to mottled red-yellow as the pollen became ripe and ready to shed (Figure 9) near the end of June. At the end of pollen release, the strobili were golden brown (Figure 9). The mature microgametophyte is a winged or bladder-like pollen grain dispersed by wind.

The female seed cones developed below and adjacent to the new terminal bud which was also enlarging at this time and became noticeable at the ends of twigs 14-18 days after the first appearance of the male cones (Figure 10), around the third week of June (Table 3). Female cones developed singly or in clusters of two to five. They became apparent as the supporting shoot elongated carrying them upward, at which time they developed their deep scarlet red-purple colour. The ovule-bearing megasporophylls spread apart for five to seven days, at approximately the same time as the microsporangiate strobilis began to shed their pollen

Table 3. Cone development dates 1978-81 for the western (H & bn) and eastern (PA & TN1) red pine stands in Newfoundland.

Stand & year	First sign of (purple) male cones	Male cones full size	First female cones	Pollination	Blue purple cones	Brown cones
H						
1978	June 12	June 16	June 20	June 27	July 23	August 12
1979	June 6	June 14	June 20	June 24	July 16	August 8
1980	June 9	June 20	June 26	June 29	July 25	August 13
1981	June 10	June 21	June 27	June 28	July 25	-
Range in days	7	8	8	6	10	6
BN						
1978	June 13	June 16	June 21	June 26	July 24	August 12
1979	June 8	June 15	June 21	June 26	July 26	August 6
1980	June 9	June 21	June 25	June 29	July 25	August 13
1981	June 9	June 21	June 26	June 29	July 25	-
Range in days	6	7	6	4	3	8
PA						
1978	June 12	June 22	June 22	June 29	July 26	August 13
1979	June 10	June 21	June 20	June 27	July 25	August 17
1980	June 12	June 21	June 21	June 27	July 25	August 15
1981	June 11	June 20	June 22	June 25	July 25	-
Range in days	3	3	3	5	4	5
TN1						
1978	June 14	June 22	June 22	June 27	July 25	August 15
1979	June 11	June 20	June 21	June 27	July 26	August 17
1980	June 14	June 22	June 21	June 24	July 25	August 17
1981	June 10	June 17	June 18	June 22	July 24	-
Range in days	5	6	5	6	3	3

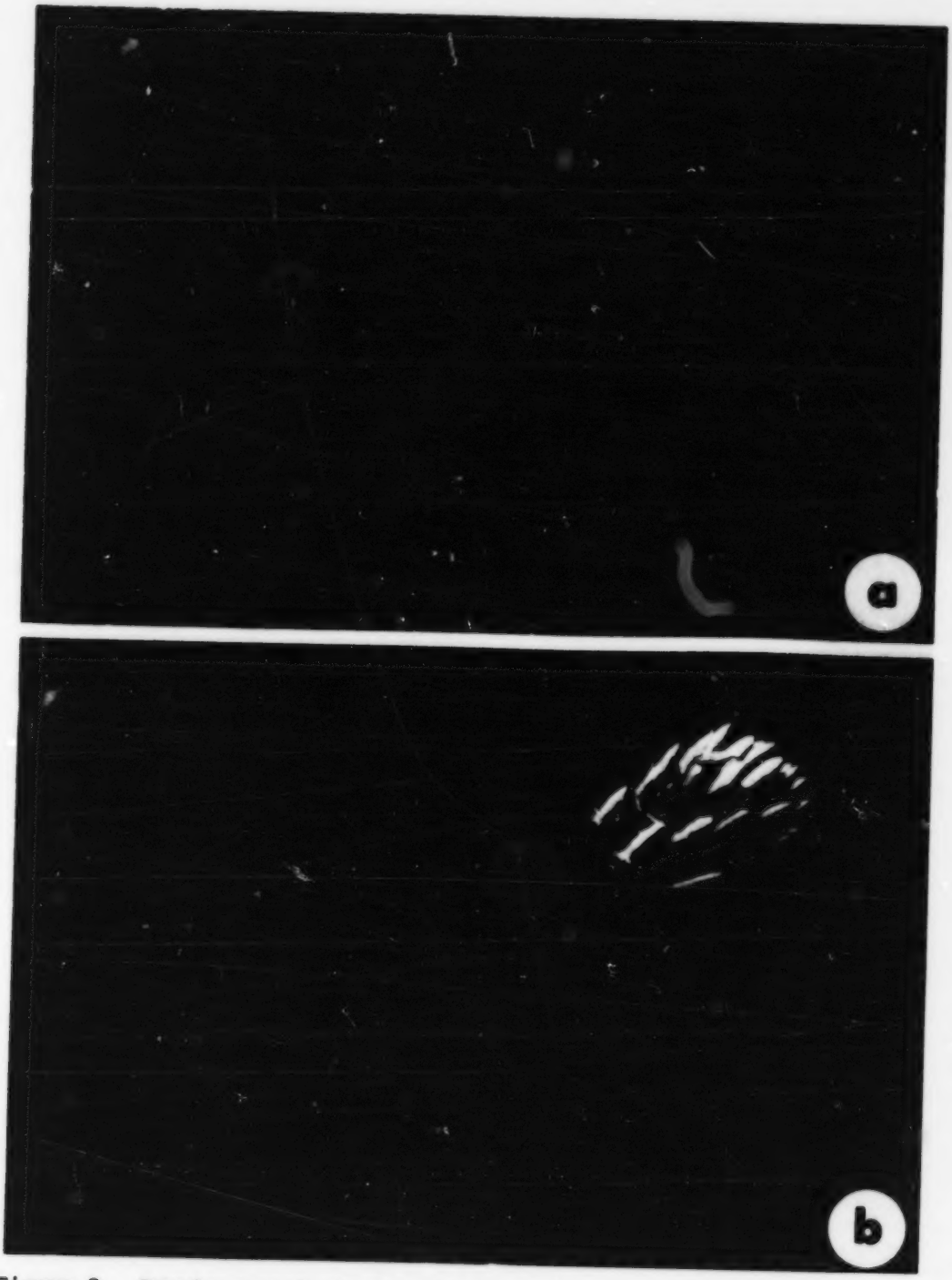


Figure 8. Developmental stages of male pollen cones of red pine in Newfoundland
(a) Male pollen (staminate) cone developing in groups around the base of vigorous twigs, June 8, PA site.
(b) Male pollen cones (x 3), purple compact, 21-22 June, PA site.

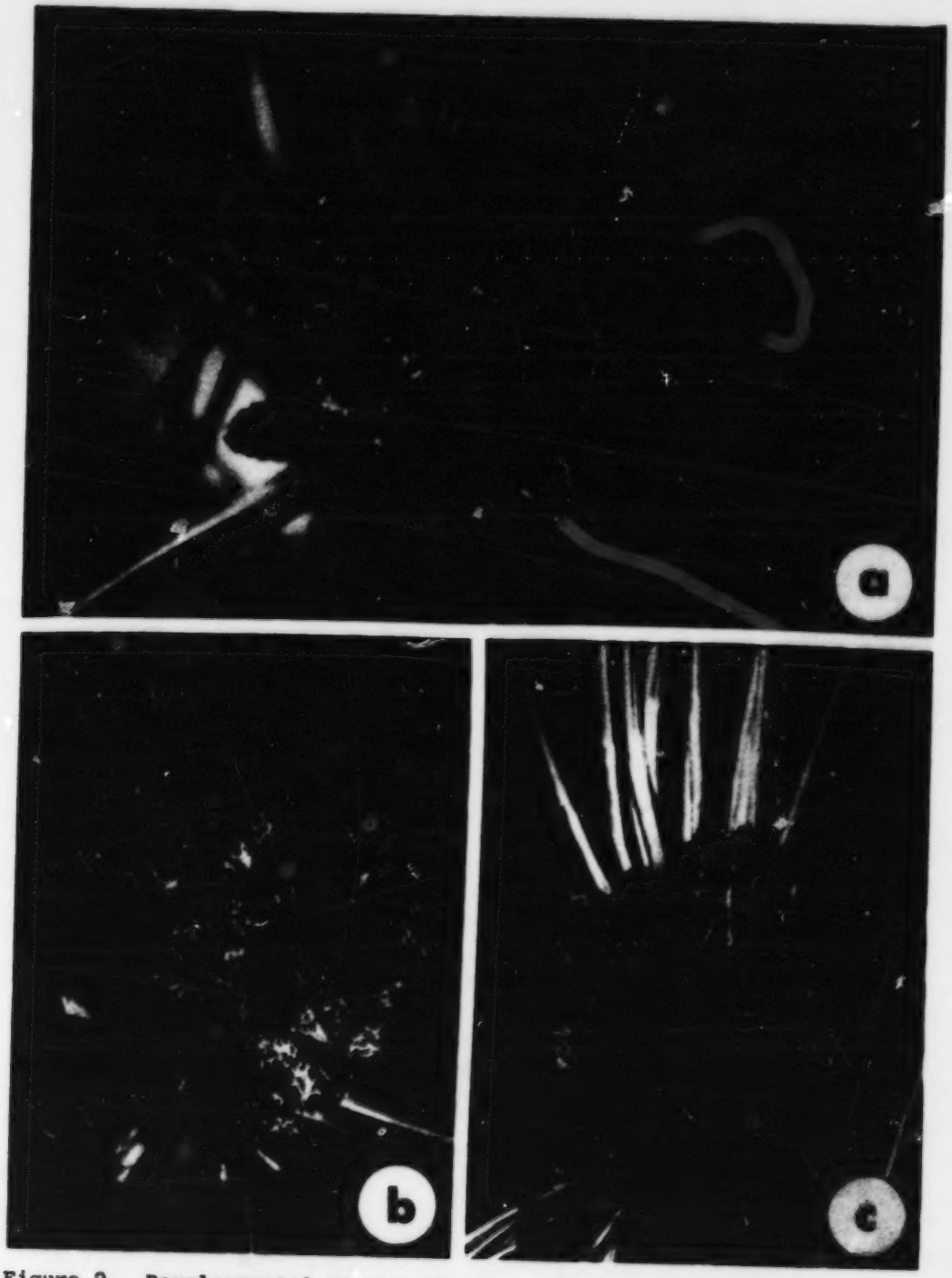
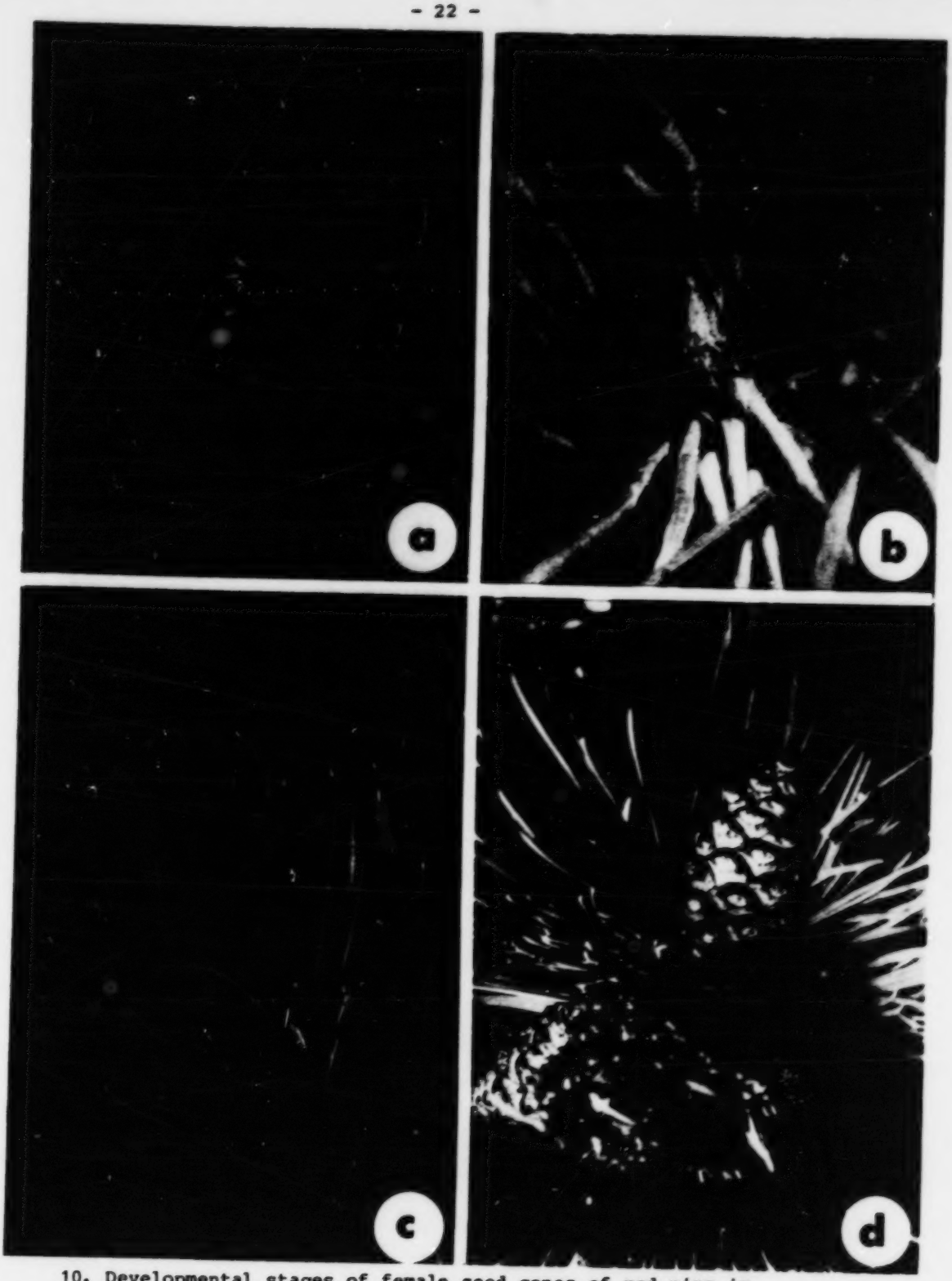


Figure 9. Developmental stages of male pollen cones of red pine in Newfoundland
(a) Swollen scarlet red staminate cone, 25-27 June, PA site.
(b) Mottled red-yellow pollen cones as they become ripe and start to shed pollen grains, 27 June, PA site.
(c) After pollen grains shed the pollen cones or staminate strobili are golden brown. One week after shedding, PA site.



10. Developmental stages of female seed cones of red pine in Newfoundland .
    (a) Female seed cones develop at the ends of twigs 14-18 days after the staminate flowers first appear, PA site.
    (b) Closed blue female conelet which has entrapped the male pollen, 26 July, PA site.
    (c) Overwintering conelets which have turned brown, PA site.
    (d) Semi-mature green cone almost fully grown 4-5 cm long. First week of August, PA site.

(near the end of June). The megasporophylls closed, entrapping the pollen grains, and then female conelets changed from a scarlet purple (third week of June, Table 3) to a darker blue purple (Figure 10) by 25-29 July. Fertilization does not take place until the mid-point of the following growing season (Lyons 1956) 13 months after pollination (Dickman and Kozlowski 1969). The female conelets enlarge slightly and change from dark blue purple at the end of July to a light brown, the state in which they overwinter (Figure 10). One can then assess the cone crop for the next year, and observe whether the cones on each branch will be single or multiple. There are usually a few degenerate cones observed by this stage.

In the second (following) year, the conelets develop rapidly from 1.0-1.5 cm long at the end of May, to 2.4-2.9 cm (base of shoot, (Figure 7)) by the end of June, and to 3.6-4.0 cm by the end of July, or early August (Figure 10). They change from green to purple-brown by September of the second growing season, and are then about 4-5 cm long. By the end of September to mid-October, the seeds are ripe and are ready to be shed.

In central Wisconsin the seasonal growth of first year ovulate strobili (1/40 the weight, 1/30 the volume and 1/3 the length of the mature cone dimensions)(Dickman and Kozlowski 1971) are all greater than the average recorded in this study. In Newfoundland, first year ovulate strobili (seed cones) averaged 1.2 + 0.2 cm for the best quality stands which is about 1/4 of the 5 cm length of the mature cone. In poorer

stands, first year ovulate strobili were often 0.7-0.9 cm and grew to about 4 cm at maturity.

The cone growth of red pine in Newfoundland is presented in Figures 8-10. There was little difference in the pollen release dates or cone development in the four Newfoundland red pine stands. Stands in the western part of the Island produced male pollen cones and female seed cones and ripe pollen three to four days ahead of the more centrally located stands in two of four years of measurement and observations. In all four years (1978-81), however there were only slight differences in the mean monthly temperatures for the two meteorological stations closest to the stands (Table 4). There were some differences in mean annual

Table 4. Mean monthly temperatures (°C). April-September from 1978-81. Column A - Deer Lake Station; Column B - Terra Nova Park Station.

Year	April		May		June		July		August		September	
	A	B	A	B	A	B	A	B	A	B	A	B
1978	0.3	NA	6.6	NA	13.3	12.3	16.0	15.9	14.6	NA	8.2	10.3
1979	3.3	1.3	10.2	NA	14.2	NA	16.8	NA	15.9	16.4	11.2	12.0
1980	2.6	2.1	5.9	5.8	10.6	12.3	13.8	11.2	13.3	9.0	9.4	11.2
1981	1.1	3.6	7.6	9.2	11.5	12.1	15.1	16.5	15.0	16.0	12.3	12.0

Data Source: Atmospheric Environment Service, St. John's, Newfoundland. Initially hair-thermohygrographs were set up in each site to record stand temperatures and relative humidity however recording equipment was constantly disturbed and vandalized.

temperatures between areas but there was little difference in the 30-year average frost-free period or growing degree day above 5°C (Roberts 1983).

In Newfoundland a delay of 21-28 days is found in all phases from bud break to pollination to maturity compared to cones and seeds from Ontario (Horton and Bedell 1960). Fowler (1965) indicated that such a three to four week time-lag for reproduction is to be expected in the extreme parts of the red pine range.

In Newfoundland the majority of red pines are open grown with limbs and main branches extending almost to the ground, and thousands of microsporangiate or pollen cones are produced on each tree (Figure 8). In a few of the more shaded lower crowns, the development of male cones was delayed as much as 30 to 40 days after the majority of the pollen cone strobili in the bright light had matured. Female seed cones are formed only at the end of twigs in bright light. Pollination is usually a prerequisite to mature cone development and fertilization is necessary for the production of viable seeds (Fowler 1965).

Seed Production

Table 5 summarizes cone and seed statistics derived for 15 of the 22 red pine stands. Stand code names are the same as in Table 1. The statistical analyses comprised the calculation of population means and standard deviations for cone measurements and germination data and were subjected to the Student-Newman-Keul's test (Sokal and Rohlf 1969) where multiple comparisons among means based on equal sample size were tested. Table 6 ranks the 15 stands in terms of smallest to largest

Table 5. Cone and seed statistics for 15 natural red pine locations in Newfoundland.

Location	No. ob. Cones/L	Cone Length (cm)	Cone Width (cm)	Cone Oven-dry Wt. (g)	Total Full* Seed	Unfertilized Seeds**	Wt. of 1000 Seeds (g)	Percent Germination	% Emerged in Sand Pots, Greenhouse
H	38	5.09 ± 0.33	2.67 ± 0.15	7.24 ± 0.90	51.3 ± 8.9	79.8 ± 11.1	5.12	91.2	40
SL1	38	4.72 ± 0.27	2.52 ± 0.13	5.58 ± 0.65	43.1 ± 8.8	89.3 ± 8.5	5.40	80.0	30
SL2	44	4.70 ± 0.35	2.36 ± 0.14	5.06 ± 0.94	31.8 ± 12.4	104.2 ± 11.4	5.40	88.0	20
SL3	36	4.74 ± 0.19	2.64 ± 0.12	6.14 ± 0.69	48.9 ± 9.8	76.2 ± 13.1	5.36	91.6	72
BN	50	4.28 ± 0.35	2.36 ± 0.22	4.50 ± 1.18	23.5 ± 10.7	103.0 ± 14.9	4.50	47.2	24
OS	59	4.03 ± 0.38	2.12 ± 0.17	3.43 ± 0.70	10.4 ± 4.8	115.3 ± 11.7	5.41	42.0	20
RB	44	4.46 ± 0.30	2.56 ± 0.14	5.68 ± 0.81	40.6 ± 11.6	57.4 ± 16.4	5.36	92.0	90
ER	52	4.20 ± 0.75	2.49 ± 0.22	5.94 ± 0.66	27.0 ± 9.5	92.8 ± 15.4	7.84	90.4	92
CA	31	4.13 ± 0.44	2.46 ± 0.24	5.29 ± 1.53	31.2 ± 13.3	90.0 ± 18.5	6.28	80.4	40
DSP	41	4.52 ± 0.39	2.49 ± 0.19	5.28 ± 1.15	35.1 ± 13.8	50.8 ± 13.3	5.86	76.8	64
MB	46	3.98 ± 0.35	2.45 ± 0.46	4.82 ± 0.73	25.2 ± 8.3	103.5 ± 12.4	4.80	64.0	72
PA	31	5.12 ± 0.35	2.68 ± 0.14	7.82 ± 1.58	43.7 ± 10.8	27.2 ± 7.5	6.87	93.6	72
TT	46	4.48 ± 0.32	2.62 ± 0.26	6.88 ± 1.49	46.8 ± 17.2	90.6 ± 14.0	5.28	82.0	60
GP***	-	4.19 ± 0.32	3.08 ± 0.33	4.95 ± 1.00	5.4 ± 5.0	79.4 ± 15.6	4.40	38.4	52
TN	31	4.48 ± 0.43	2.62 ± 0.25	6.37 ± 1.44	37.2 ± 18.0	62.8 ± 17.6	7.22	78.8	64
MEANS ± S.D.	41.9 ± 8.4						5.67 ± 0.98	77.1 ± 16.7	54.8 ± 23.2

*Prior to 1987 all cones collected were insect and disease free.

**As determined by the presence of wings.

***Spring cone collection; all the rest fall collections.

Table 6. Cone and seed statistics from 15 red pine locations ranked by placing the means in numerical order by the Student-Newman-Keul's test. The lines indicate means that are not significantly different at the five percent level.

	Cone Length	Cone Width	O.D. Weight	Total Seeds	No. of Wings
1	MB	OS	OS	GP	PA
2	OS	SL2	BN	OS	DSP
3	CA	BN	MB	BN	RB
4	GP	MB	GP	MB	TN
5	ER	CA	SL2	ER	SL3
6	BN	DSP	DSP	CA	GP
7	RB	ER	CA	SL2	H
8	TT	SL1	SL1	DSP	SL1
9	TN	RB	RB	TN	CA
10	DSP	TN	ER	RB	TT
11	SL2	TT	SL3	SL1	ER
12	SL1	SL3	TN	PA	BN
13	SL3	H	TT	TT	MB
14	H	PA	H	SL3	SL2
15	PA	GP	PA	H	OS

values for each parameter, i.e., the means are arranged in order of magnitude and the lines beside them represent nonsignificant different sets of means. Any pair of means enclosed by the range of any one line in the second convention is not significantly different at the five percent level.

These statistical tests indicate a number of consistencies. The smallest stands (Table 1) e.g., BN, OS, ER, MB, tended to produce the smallest cones, with the OS stand consistently having the lowest in terms of cone size, cone oven-dry weight, number of seeds produced per cone, and the highest in terms of unfertilized seeds. OS is the smallest stand (Table 1) and is also the oldest and the poorest stand (RP3) type (Roberts and Bajzak 1984). Besides producing the least number of full seeds (5-15 per cone) and the highest number of wings without full seeds (100 per cone) it also had the lowest seed viability. Conversely, the largest stands produced larger cones, with the highest number of full seeds (40-50 per cone), and the lowest number (27-90 per cone) of wings without seeds. The heaviest or largest seeds tend to have come from the best quality (RP1 and RP2) stands, e.g., PA or TN; however, the two stands from geographic area II (ER and CA) had the heaviest and fourth heaviest 1000 seed weight. The Charles Arm seaside site had cone and seed statistics in the mid-range of measurements. The ER stand produced a very small number of seeds per cone, but they were very large and had among the highest viabilities; positive correlation of seed weight and viability in red pine has been reported (Dhir 1971).

Simple correlation analysis were performed on the oven-dry weight cone against total full seeds per cone and weight of 1000 seeds against germination percentage. These analyses produced positive correlations with r^2 values of 0.714 and 0.712 respectively (GP site (Table 1) omitted). The variation as exhibited by the high standard deviations for

each of the 15 red pine sites was the reason for the low r^2 values. In Wisconsin, the number of full seeds per cone was also positively correlated with cone volume and dry weight (Dickman and Kozlowski 1971). Mean cone dry weights varied from 6.9 to 9.4 g in Wisconsin compared with 3.7 to 7.8 g in Newfoundland.

In testing red pine seed lots from a wide range of natural soils Youngberg (1952) concluded that seed from red pine that grew on infertile soils was generally of poor quality. Fertilizing with ammonium nitrate improved red pine seed production in Ontario (Cayford and Jarvis 1967) as did a balanced NPK fertilizer application in Manitoba (Dyck 1985; Owens and Blake 1985). This indicates the importance of the site quality in seed production.

In Newfoundland the large number of wings without seeds in all stands was expected. Lyons (1956) reported that the seed capacity of red pine cones varied from 30 to more than 110, depending on the size of the cone and its position in the tree crown, and was determined by the number of ovules that were structurally complete at the time of pollination. These ovules occurred in a central productive region of the cone which usually constitutes less than one half the total potential seeds. The abortion of ovules in the productive region of the cone usually reduced seed production efficiency to 50-60%, and was accompanied mainly by withering of the nucleus in the first year with failure to produce archegonia early in the second year (Lyons 1956). The most common cause of late ovule abortion in conifers is the lack of pollen (Owens and Blake 1985) but Lyons (1956) suggested that competition for nutrients may be a factor

leading to abortion of already pollinated ovules. Developing seed cones constitute strong metabolic sinks competing for finite amounts of nutrients (Owens and Blake 1985). Thus a general increase in tree vigor may increase cone and seed production. This appears to be borne out by the present study where nutritional differences between the best (PA) and the poorest site (OS) were quite significant. The open-grown nature of the Newfoundland red pine stands also helps cone production and there was pollen produced in all stands. Generally there was a tendency for the cone crop size to increase with an increase in dbh. However, the largest trees in a special plantation study in Ontario did not always bear the most cones (Stiell 1988).

Khalil (1984) reported that in Newfoundland black spruce cone length, cone diameter, and cone oven-dry weight were under strong genotypic control, but most cone and seed characteristics were under both genotypic and environmental control. Cone size has been found to decrease with increasing distance from the apex of the tree in several coniferous trees (Khalil 1984) including red pine (Lyons 1956). Picking cones from the same upper crown portion in the present study was standardized, hence, the environmental conditions of the stand in terms of stand quality and size as related to cone and seed production are probably quite meaningful.

In seed tests of Newfoundland red pine from the DSP site at Gambo in the early 1970s, Wang (pers. com.) reported that the seed yield was about half the Ontario average, and X-ray radiographs showed many underdeveloped embryos and 70-80% polyembryony, most likely resulting

from inbreeding or poor weather conditions as well as from growth in a small population. In this study this site produced an average amount of seed (35 per cone) with 76% germination. There were more than 50 unfertilized seeds per cone from this site (Table 5).

Regeneration Survey

The results of the regeneration survey show that the stands without any physical disturbance or recent wildfire have few regenerating red pine. The surface substrates are completely occupied in these stands by dense ericaceous shrubs. Medium to good regeneration was observed and measured in the H, SL1 and SL2 sites where physical scarification from transmission line corridors and a 1977 wildfire (Roberts and Janes 1982; Roberts and Mallik 1987) have provided adequate seedbed conditions. The BN and ER stand, both partly destroyed by gravel extraction, showed the greatest numbers of regenerating red pine, and more than 200 seedlings from age 1-5 were counted in ten 1 m^2 quadrats checked every 10 m on a 100 m transect. Regeneration was very poor in the RB stand, where more than 80 years have passed since the last wildfire and the forest floor is covered with dense ericaceous shrubs (Figure 6c). In the largest stand (PA), regeneration was good prior to the 1979 wildfire. The openings created by a 1946 wildfire were regenerating, and some areas disturbed by gravel extraction had adequate regeneration. Most of the trees, which ranged in height from 0.5-7.0 m were, were killed in the 1979 wildfire. Currently natural regeneration in some parts of the PA site showed adequate seedling populations eight years after fire. The Terra Nova and Traytown stands have medium regeneration but many of the seedlings,

especially the 0.5 m size, are removed annually by the public for transplanting to household gardens. In the Traytown site more than 100 holes were counted where trees have been removed.

In a study of seedling and nuclear characteristics of the DSP seed lot, Dhir (1971) reported that the red pine seedlings were characterized by very poor growth, particularly of roots, and hence survival of seedlings would be less than in other areas. Seed weight, mean shoot and root weights were lower than the 14 other Canadian and American seed lot sources tested.

The poor yield and viability of seed from some stands of Newfoundland red pine along with poor rooting characteristics possibly account for generally sparse regeneration in the small stands. In larger stands that produce adequate seeds, the lack of regeneration can be better explained by the site characteristics of each stand. Red pine germinated or grew poorly in its own and several other seedbed materials (mainly litters) in Minnesota which reflects its requirements for mineral soil seedbeds for natural seedling establishment (Ahlgren and Ahlgren 1981). The scarified areas in Newfoundland red pine stands contained the most regeneration and supports the above suggestion. Recent work of laboratory experiments on seed germination and seedling growth of red pine on organic matter and mineral soil also supports this view (Mallik and Roberts 1987).

Red pine is also known to be sensitive to soluble extracts of a number of ground species, which suggests an allelopathic relationship (Norby and Kozlowski 1980). Kalmia angustifolia, one of the main forest

floor species in Newfoundland, is also known to be allelopathic (Mallik 1987). The thick ericaceous mor humus in some stands with the large volumes of rhizomes is also likely to be a strong physical barrier to red pine seedling establishment in Newfoundland.

CONCLUSIONS

1. Comparisons of phenology between Newfoundland and Ontario showed that in Newfoundland there is a time lag of 21-28 days in all phases from bud break to pollination to maturity of cones and seeds compared to Ontario due to late spring conditions.
2. Newfoundland red pine, although diminishing in numbers today, produce adequate seed crops with adequate seeds (10-50 seeds per cone) with 38-94% viability.
3. The better quality stands usually produce the best cone crops and the best quality seed.
4. There are only very minor differences in cone development from the western most stands to the eastern most stands due to similar climate within the range in Newfoundland.
5. The lack of red pine regeneration in Newfoundland can be attributed to poor seedbed conditions. The thick ericaceous mor humus and the dense Kalmia understory vegetation has both a physical and allelopathic effect on regeneration. In addition the severe competition from the more shade tolerant black spruce has also contributed to the decline of red pine in Newfoundland.

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